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FRUGIVORY OF SALVIN'S CURASSOW IN A RAINFOREST OF THE COLOMBIAN AMAZON

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ABSTRACT.—We report the diet and the fate of seeds ingested by a family group of Salvin's Curassow (*Mitu salvini*) in Colombian Amazon. The study group consumed 123 plant species from 41 families. Of these, 106 species provided fruits, 21 seeds, 7 cotyledons, 19 flowers, and 9 leaves. Many species of invertebrates and vertebrates were also consumed. During the 14 months about 70% of the diet of each individual was composed of fruits. However, there was considerable temporal variation in diet composition and fruits were not always the most exploited item. Salvin's Curassow acts mainly as a seed predator (67% of the species eaten) on seeds longer than 5 mm but as a seed disperser (28% of the species eaten) for seeds shorter than 5 mm long, which were only rarely and opportunistically exploited. The remaining fruits eaten (5% of the species consumed) were neither dispersed nor predated. As a result of our study, we propose that Salvin's Curassows are mainly seed predators because most seeds ingested by the study group were preyed upon, and seed size was critical in determining seed fate. *Received 14 March 2000, accepted 22 August 2000.*

Curassows, chachalacas and guans (family Cracidae) are large Neotropical forest-dwelling birds that reach their greatest diversity in the Amazon region (del Hoyo et al. 1994, Strahl et al. 1997). They are an important component of the avian biomass in Neotropical bird communities (Terborgh 1986a, Strahl et al. 1997) and provide substantial amounts of protein for rural and Indian people (Silva and Strahl 1991, Vickers 1991, Thiollay 1994). Being extremely sensitive to overhunting and deforestation, cracids are one of the most threatened bird groups in Latin America (Collar et al. 1992, Galetti et al. 1997, Strahl et al. 1997) and can therefore be used as indicators of these two forms of human activity (Silva and Strahl 1991, Strahl and Grajal 1991).

The role of Curassows in seed dispersal and predation is unclear (Levey 1994). Some authors considered them fruit pulp consumers and assumed them to be high quality seed dispersers (Silva and Strahl 1991, Strahl and Grajal 1991), whereas other authors reported them to be important seed predators (Moermond and Denslow 1985, Érard and Sabatier 1986, Terborgh 1986a, Peres and van Roosmalen 1996).

The Salvin's Curassow (*Mitu salvini*) is a large (ca 2.5 kg), terrestrial cracid that occurs in southwestern Colombia, eastern Ecuador, and northeastern Peru (Delacour and Amadon 1973, del Hoyo et al. 1994, Strahl et al. 1997). Little is known about its natural ecology (Santamaría and Franco 1994, Jiménez et al. 1998, Yumoto 1999) or its population densities (Hedemark Jonhson 1993, Santamaría and Franco 1994).

Here we report the feeding ecology and the fate of seeds ingested by a family group of Salvin's Curassows. This constitutes the first long-term study on curassows based on direct field observations.

METHODS

Study site.—The study was carried out on the eastern border of Tinigua National Park, in the northern Colombian Amazon. The base camp was located in lowland tropical rainforest on the west bank of the Duda River (2° 40′ N, 74° 10′ W, elevation 350 m). A riparian forest occurs along the banks of the river but is replaced towards the interior by a forest that is inundated during the rainy season. The terrain in the higher zones is undulating, drained by small channels and is basically a terra firme habitat with a 20–25 m canopy. Annual rainfall is approximately 2600 mm and highly seasonal, with a dry season from December to March. The average minimum and maximum temperature are 21.1° C and 28.7° C (Hirabuki 1990, Kimura et al. 1994, Nishimura et al. 1995). Phenology data obtained between March 1990 and February 1991 indicate that fruit production varies seasonally in the study area, peaking in April, followed by a gradual

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decline, reaching its lowest abundance at the end of the rainy season in November (Stevenson et al. 1998).

Study group.—Observations were focused on one pair of *Mitu salvini* that had been habituated to observers between August 1990–July 1991. Despite the physical similarity between males and females, individuals were identified by subtle morphological characters (smaller body and bill in the female) and sex-specific vocalizations. The pair moved through the forest together, usually with the male in the lead. The home range was approximately 150 ha and food was obtained primarily from the forest floor (Santamaría and Franco 1994). A chick hatched in April 1993 and remained with the pair for ten months (February 1994) until the adults aggressively expelled it.

The field study was conducted between September 1992 and February 1994 and included a single reproductive cycle of the pair: the pre-reproductive period (October–November 1992), the reproductive period (January–April 1993), and the chick rearing stage (May 1993–February 1994). No observations were made in December 1992 and July–August 1993.

The family group was observed from 5:40/6:00 to 17:30/18:20, from 3–5 meters away. Throughout the day, data were recorded using a focal sampling method (Martin and Bateson 1993). Observations were alternated daily among male, female, and young, resulting in three to seven days of observation per individual per month. In total, 2522 hours of observation were accumulated over 185 days.

Diet composition.—Foods ingested by the group were classified into fruits, seeds, cotyledons, flowers, leaves, animals (vertebrate and invertebrate), unknown material, and other. The category other included roots, water, stones, and earth [soil and earth from ant nests (*Atta* sp.)].

Monthly diet composition was estimated by recording the time invested in foraging on each food category (expressed in percentages). This was based on a continuous sampling (Martin and Bateson 1993) of the foraging activity of focal individuals. This activity included searching for and consuming food items. Curassows repeatedly visited a foraging patch and remained there for different amounts of time (Santamaría and Franco, unpubl. data). A foraging patch is defined as the projected area of the tree producing food.

Diet diversity.—Each tree used by the group was marked with a numbered label. Botanical collections were made for species identification by specialists. Invertebrate samples were preserved in 70% ethanol for later identification. The data on diet diversity were complemented by observations of the authors conducted on the same pair between August 1990–June 1991.

Seed dispersal and predation.—Fecal samples (n = 1245) from the focal individual were gathered daily (n = 185 days). Seeds were retrieved by straining the feces through 0.5 mm brass sieves and identified against a reference collection. Because *Mitu salvini* does not regurgitate seeds, all seeds contained in the fecal samples were considered to be dispersed, whereas seeds from consumed fruits that did not appear in the feces were classified as preyed upon. Here, the quality of the dispersion by these birds is not considered because the viability of dispersed seeds was not studied. Because seed length seemed to affect the fate of seeds ingested, we measured seed lengths from Curassows' feces, the foraging patches, and used lengths in the literature (Stevenson et al. 1999).

RESULTS

Composition and temporal variation in diet.—About 70% of each individual's diet was composed of fruits, 10% of seeds, and each of the other categories each less than 5%. This pattern varied month to month and among individuals. For both the male and female, the time foraging for fruits varied from 60–96% during ten months of the study (Fig. 1A, B). Diet composition differed dramatically during two separate two-month intervals. In April–May 1993, the time spent foraging for seeds and cotyledons increased while the time foraging for fruits decreased. In January–February 1994, fruits and seeds were ingested in similar proportions of time, while the amount of time foraging for animals increased considerably (Fig. 1A, B).

The time spent foraging for leaves was low (0.5–6%) but constant, while the time invested in ingesting flowers varied seasonally (Fig. 1A, B). In October–November 1993 and 1994, the time foraging on flowers increased because the group intensively foraged on inflorescences of *Carludovica palmata* (Cyclanthaceae).

During the first months of the chick's development (April–May), its diet was composed primarily of animals (24–38%), cotyledons (15–28%), fruits (16–26%), and seeds (9–12%; Fig. 1C). Thereafter, its diet was similar to those of the adults. During five months the birds spent much time foraging for fruits (70–91%), while in two months (January–February 1994) they showed an increase in time spent foraging for animals (6–18%) and fruits and seeds (36–42% and 36–38%, respectively; Fig. 1C).

Diet diversity.—A total of 123 plant species, representing 41 families, was exploited by the group. Of these, 106 species were recorded for fruits (ripe and unripe), 21 for seeds (ripe and unripe), 7 for cotyledons, 19 for flowers, and 9 for leaves (Table 1). The family containing the largest number of spe-

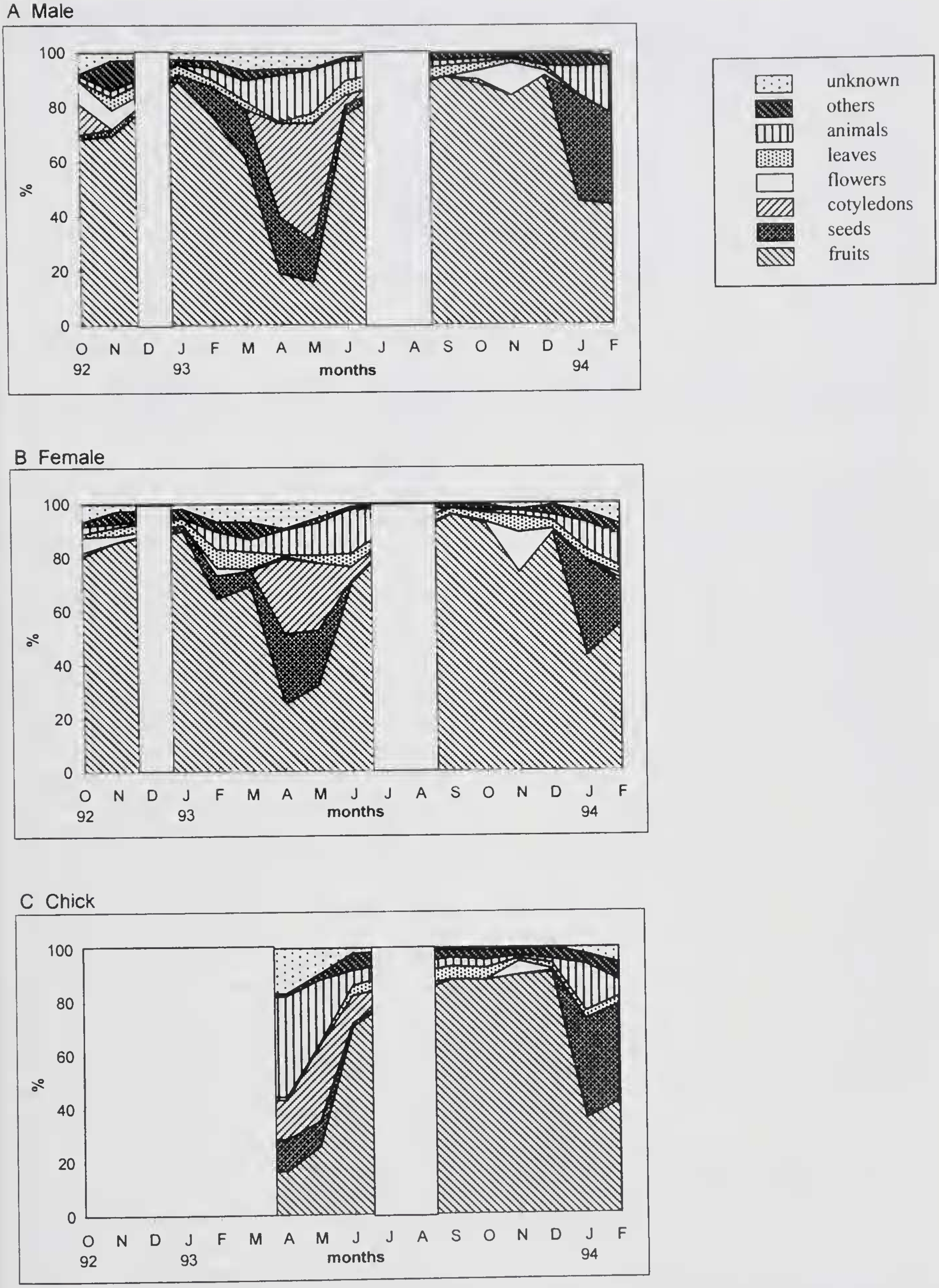

FIG. 1. Monthly variation in the percentage of time foraging on different food categories per individual October 1992–February 1994.

TABLE 1. Number of species per family exploited and food types consumed by the study group August 1990–June 1991 and October 1992–February 1994.

Family	No. of species	Food category[a]
Acanthaceae	2	Fl, L
Annonaceae	2	F
Apocynaceae	4	F, S, C, Fl
Araceae	6	F, Fl
Arecaceae	6	F, Fl
Araliaceae	1	F
Bignoniaceae	2	F, S
Burseraceae	4	F, S, C
Capparaceae	3	F, Fl, C
Caricaceae	1	F, Fl
Cecropiaceae	5	F, S, C
Commelinaceae	1	F
Clusiaceae	3	F, S, Fl
Costaceae	2	F
Cyclanthaceae	1	F, Fl
Euphorbiaceae	1	F
Haemodoraceae	1	F, Fl
Heliconiaceae	4	F
Hippocrateaceae	1	F
Lauraceae	4	F
Lecythidaceae	2	F, S
Marantaceae	3	F, Fl
Melastomataceae	7	F, L
Meliaceae	4	F
Menispermaceae	1	F
Mimosaceae	6	F, S, C
Moraceae	13	F, S, C, Fl
Myristicaceae	1	F
Myrtaceae	1	F, S
Poaceae	1	S
Polygonaceae	1	F
Rubiaceae	12	F, Fl, L
Sapindaceae	3	F
Sapotaceae	3	F, S
Sterculiaceae	3	F
Strelitziaceae	1	F
Solanaceae	1	F
Theophrastaceae	1	F
Tiliaceae	1	F
Verbenaceae	1	L
Violaceae	3	F, S, Fl

[a] Fl = flower, L = leaf, F = fruit, S = seed, C = cotyledon.

cies exploited for fruits (13), seeds (5), and cotyledons (2) was Moraceae. Rubiaceae fruits were represented with 11 species. The greatest number of species used for flowers and leaves were in the Arecaceae (4) and Rubiaceae (3) families, respectively.

It was possible to collect all plant species used for fruits, seeds, and flowers but not for those used as leaf and cotyledon resources.

TABLE 2. Invertebrates and vertebrates ingested by the study group between August 1990–June 1991 and October 1992–February 1994.

Invertebrates	Vertebrates
Terrestrial snails	Frogs (adult alive)
Worms	Snakes (adult alive)
Amblipigy, spiders	Pigeons (eggs)
Terrestrial crabs	Ground-Doves (eggs)
Centipede	Tinamous (chicks and eggs)
Millipede	Hummingbirds (chicks and eggs)
Beetles	Trushes (chicks)
Ants (several spp.)	Armadillos (carapace and bones)
Termites	Agouti (bones)
Moths and caterpillars	Rats (alive)
Dragonflies	Bats (dead)
Grasshoppers, buzzers, mantids	
Cockroaches	

Animals ingested could not always be identified because they were difficult to collect. Nevertheless, many animal species were eaten by the group (Table 2). Both invertebrates and vertebrates were hunted by the curassows and some vertebrate carcasses were scavenged. The carapace of an armadillo was repeatedly visited by the curassow pair before beginning incubation. The nests of several bird species were raided and eggs as well as chicks were eaten. Occasionally, the group joined bird flocks of army ant followers for up to two hours, capturing invertebrates flushed by the ants.

Feeding behavior.—Between January–June, the group followed a moving foraging pattern (sensu Zhang and Wang 1995). This behavior was characterized by patrolling various fruiting trees and remaining at each one for short periods (5–20 min). By contrast, August–December few canopy trees had large fruit crops and the group followed a stationary-feeding pattern (sensu Zhang and Wang 1995). This behavior was characterized by the consumption of fruits from a single canopy tree, with the birds remaining for 1–20 consecutive days foraging and resting under or near the tree. They also defended the foraging patch from a Black Curassow group (*Crax alector*). The stationary feeding pattern was associated with *Clarisia racemosa* (Moraceae)

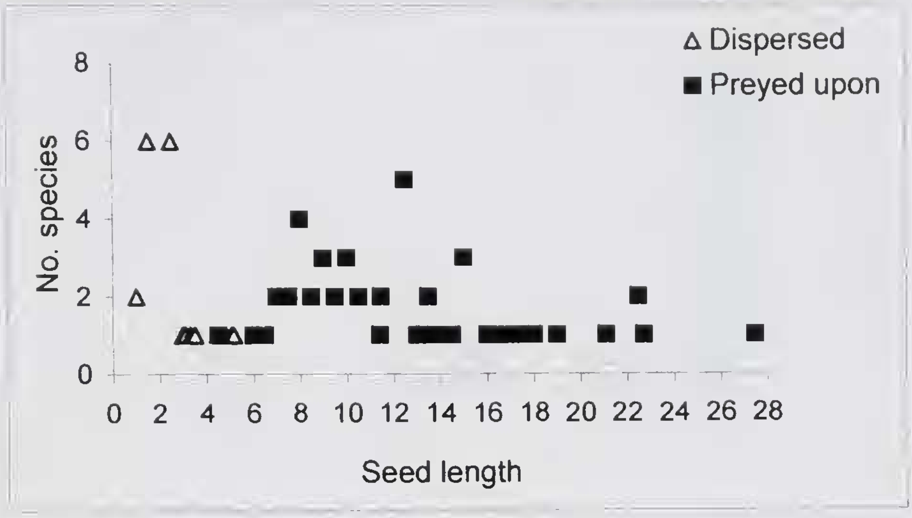

FIG. 2. Number of species dispersed and preyed upon, according to seed length. Seed lengths based on seeds taken from curassow's feces and the foraging patches and from Stevenson and coworkers (1999).

and *Cupania cinerea* (Sapindaceae; August–September 1990), *Talisia intermedia* (Sapindaceae; November 1992) and *Guarea guidonia* (Meliaceae; September–November 1993).

In October 1992, none of the canopy trees used by the curassows produced fruit within the group's home range. Their response to this scarcity was to patrol the forest daily using long transects and investing much time in foraging (an average of 8 hours) but little time in resting. *Heliconia* spp. (Heliconiaceae) fruits and *Carludovica palmata* (Cyclanthaceae) inflorescences were the principal food sources during this time.

To obtain cotyledons, curassows concentrated their foraging under a tree they had previously exploited for fruits and seeds. Typically they pulled up seedlings with their beaks and cut and ate the cotyledons, but occasionally cotyledons were consumed without pulling up the seedlings.

The cracids ate not only young leaves but also mature leaves from understory plants and forest floor. The group always ingested young and mature leaves of *Trichanthera gigantea* (Acanthaceae) after consuming fruits of *Guarea guidonea* (Meliaceae).

Fate of ingested seeds.—The whole fruit (pulp and seed) was ingested in most cases, except for six species. Of 109 fruits and seeds consumed by the curassows, 30 species (28%) of seeds were dispersed by endozoochory, 73 species (67%) of seeds were destroyed, and only the pulp was consumed in 6 species (5%).

Damaged and undamaged seeds of *Geophila macropoda, Psychotria psychotriaefolia,* and *Psychotria muscosa* (Rubiaceae) were retrieved from the feces. Large quantities of stones, red aril fragments of *G. guidonea,* armadillo shell, and insect exoskeletons were also recovered from feces. Seeds of *Gustavia* sp. (Lecythidaceae), *Inga* sp. (Mimosaceae), *Castilla ulei,* and *Pseudolmedia* sp. (Moraceae) were eaten from the ground and the feces of two primates (woolly monkey, *Lagothrix lagotricha;* spider monkey, *Ateles belzebuth*). This suggests that Salvin's Curassow is a post-dispersal seed predator.

Species that were preyed upon were characterized by having fruits with one or two large, oily seeds embedded in little pulp or surrounded by an aril. The seed lengths were 6–30 mm [$\bar{x}$ = 12.69, ± 4.78 (SD), n = 52; Fig. 2), except for *Rinorea lindiana* seeds ($\bar{x}$ = 4.5). Seventy-eight percent of species preyed upon were from canopy and subcanopy trees, 16% from understory plants, and 6% from lianas and epiphytes (Fig. 3). Several species represented a primary resource in the group's diet. During July–December (stationary feeding pattern), the group's diet consisted primarily of species whose seeds were digested (*Clarisia racemosa, Cupania cinerea, Talisia intermedia, Guarea guidonia*). In contrast, dispersed species were occasionally and opportunistically consumed. The seed lengths were 2–5 mm ($\bar{x}$ = 2.68 ± 1.27, n = 23; Fig. 2). Approximately 70% of the species were small understory plants (Fig. 3), with small,

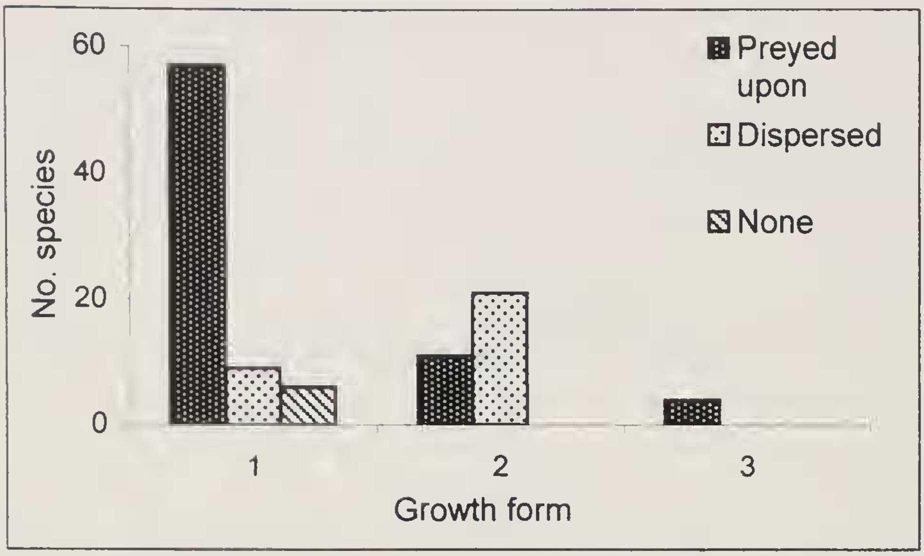

FIG. 3. Number of species dispersed, preyed upon, and not eaten (none) based on the growth form of each species. 1 = canopy and subcanopy trees, 2 = understory plants, 3 = lianas and epiphytes.

juicy fruits containing small seeds (2–5 seeds per fruit) and principally Rubiaceae. The other 30% were from trees 10–25 m tall (one hemiepiphyte species; Fig. 3), that had large fruits with many small seeds embedded in abundant pulp.

DISCUSSION

Previous researchers have classified curassows as chiefly vegetarians (Delacour and Amadon 1973, Torres 1989, del Hoyo et al. 1994), whereas others have considered them to be strictly frugivorous (Silva and Strahl 1991, Strahl and Grajal 1991); some authors reported them to be granivorous (Terborgh 1986a, Terborgh et al. 1990) or seed-eating frugivores (sensu Moermond and Denslow 1985). We found that Salvin's Curassow is mainly a seed predator, digesting the seeds of 67% of the plant species it consumed. This suggests that it is the seeds and not the pulp that is the desired food. The group had a broad diet and spent considerable time foraging for resources other than fruits. Nevertheless, group movements inside the forest seemed to be determined by the location of fruiting trees. Therefore, we suggest that this species should be considered a seed-eating frugivore (sensu Moermond and Denslow 1985) that requires other types of food (fauna, leaves, and flowers) to complement its diet and to satisfy its metabolic requirements.

The availability of high quality resources (seeds and cotyledons) coincided with the reproductive period and hatching of a chick in April. This was also the time the birds took the greatest amount of animal matter. Typically birds feed their chicks predominantly with animal protein during the first months of life to guarantee their rapid growth and development (Morton 1973). Birds require calcium for eggshell production, which can be obtained from grit and mammal bones (MacLean 1974). This could explain why, before incubation (February–March), the study group spent considerable time foraging on an armadillo carcass and bones.

Our results indicate that Salvin's Curassows have a high digestive capability. This ability is due to the powerful, muscular gizzard with a rough interior surface, which allows these birds to crush hard seeds. Small stones and coarse sand appear to serve as grit for grinding because they were always found in the feces analyzed during all of the months sampled.

Our data suggest that the fate of seeds ingested may be determined by their size. Small seeds (<5 mm) were found to pass unharmed through the digestive tract, while larger seeds (>5 mm) were destroyed. We cannot say that small seeds are not digested, but small seeds were more commonly found in the species' feces. Yumoto (1999) reported that Salvin's Curassow dispersed only 6–10% of the small seeds (<5.5 mm) it consumed from two plant species (*Geophila repens,* Rubiaceae; *Ficus sphenophylla,* Moraceae). Seed predation has also been observed in the Black Curassow (*Crax alector*; Érard and Sabatier 1986) and

Amazonian Razor-billed Curassow (*Mitu tuberosa*; Peres and van Roosmalen 1996).

Regular folivory, which is rare in birds (Morton 1978), suggests that the study group required some of the nutrients present in vegetation. Leaves are a source of proteins, but they are difficult to digest because they are high in structural carbohydrates and they contain a variety of toxic compounds (Lambert 1998, Milton 1998). The regular ingestion of soil and ant soil of *Atta* sp. by the study group could be how they deal with the toxins in the leaves. In fact, geophagy has been reported for several species of birds: parrots, pigeons, cracids, grouse (Diamond et al. 1999). Soil ingestion might help grind ingested food, absorb plant toxins, acquire essential minerals, and buffer acidic or alkaline foods (Diamond et al. 1999). Detailed analyses of digestive physiology of this curassow are needed to test the various roles suggested for soil consumption.

The phenology of the plants in the study area in 1990–1991 (Stevenson et al. 1998) indicates that fruit production varies seasonally, peaking in April and reaching its lowest abundance in November. The two feeding behaviors used by the study group appear to be related to the pattern of fruit availability. During the period of fruit abundance (January–May), when there was a high diversity of potential foods, the group moved over a large area and hence incorporated a large variety into its diet. By contrast, the group moved little during the period of low fruit supply (September–December). When food was scarce, the cracids would exhibit a conservative strategy by moving less and concentrate their foraging around a guaranteed source of food.

Frugivorous vertebrates (especially birds, bats, and primates) are believed to play a central role as seed dispersers in the natural regeneration of tropical forests (Estrada and Coates-Estrada 1986, Willson et al. 1989, Julliot 1997). Cracids may be important in tropical forests dynamics, not just as seed dispersers but also through seed predation (Érard and Sabatier 1986, Strahl et al. 1997). Repeated foraging in the same patch for fruits, seeds, and cotyledons would diminish the concentration of seeds and seedlings under those trees and affect the distribution of those species.

Although *Ficus* species have been reported to be important for frugivorous vertebrates in some lowland tropical forests (Leighton and Leighton 1983, Terborgh 1986b), they do not appear to be important to *Mitu salvini,* at least in our area. *Ficus* fruits were consumed rarely and opportunistically by the study group. Fruits of other tree species were intensely exploited (e.g., *Guarea guidonia*) and may serve as the primary food for this cracid as well as other non-passeriform birds during the period of food scarcity.

Few field data on natural populations of cracids have been collected; hence, basic information on which to base effective management plans for these birds is still missing (Brooks and Strahl 2000). Some researchers (Silva and Strahl 1991, Borges 1999) suggest that hunting may have a greater impact on cracid populations than habitat degradation but we still do not know. The survival of this commonly hunted species is threatened in the Neotropics (Brooks and Strahl 2000). As a result, there may be little opportunity to assess how cracids use these habitats and influence community dynamics. In the case of Salvin's Curassow, its future seems uncertain at least in the study area as human colonization advances rapidly bringing with it hunting and habitat degradation.

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